

Capillary Electrometer Records of the Electrical Changes during the Natural Beat of the Frog's Heart. (Preliminary Communication.)

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It was shown, in 1880, by Burdon-Sanderson and Page, that when the ventricle of the excised frog's heart is connected with a capillary electrometer by two contacts, one lying on the base and the other on the apex, then every contraction of the heart was associated with electromotive changes of the following type. The electrometer meniscus was displaced in a given direction, the displacement then suddenly returned and, after a certain time, a second final displacement occurred in the opposite direction, which returned slowly; the recorded displacements are therefore of the type shown in fig. 1 of the annexed diagram. Most of these earlier experiments were carried out on the excised heart rendered motionless by a suitable ligature around the sino-auricular junction, and excited to activity by an induced current which was applied to the tissue, near one of the electrometer contacts. The observed effects were demonstrated to be due to the algebraic sum of an active process under one contact, of the propagation of this process to the tissue under the other contact, and of the occurrence of a similar active process at this further point. The two phases, such as occur in fig. 1, were further shown to be indicative of the time relations of these active processes. The electromotive change during the active process causes this tissue to become relatively negative as compared with the inactive tissue. This negativity commences under the proximal contact, nearest to the seat of excitation; its development is, however, cut short by a similar change occurring under the distal contact situated further off from the seat of excitation, thus giving the first electrometer displacement the character of a single spike. Whilst both changes are in full progress there is no electrical difference between the contacts, and thus an iso-electrical interval occurs; finally, the change at the proximal contact, having commenced first, ends first, and the distal change outlasting the proximal one, a terminal displacement of opposite sign is produced. All these well-known results have been supposed, with little experimental warrant, to occur in the beating frog's heart *in situ*, and a discrepancy thus exists between the assumed electromotive phenomena of the beating frog's heart and the electrical changes actually observed in the beating heart of mammals and of man. Numerous records have been obtained in man and mammals by making use of Waller's

discovery that the electrometer, when appropriately connected with the surface of the body, shows the electromotive changes which accompany each beat of the heart *in situ*. These have been supplemented by observations upon the exposed beating heart (Bayliss, Starling, etc.). The latest records of this type in the case of man are those which Einthoven has obtained by the use of his delicate string galvanometer. All these records differ fundamentally from the records obtained by Burdon-Sanderson with the excised heart of both the frog and the tortoise, for, although the effects are diphasic, the second phase in the mammalian heart is of the same sign as the first (as in fig. 2), instead of being of opposite sign. It has thus been suggested that there is a want of parallelism between the activities of the mammalian heart and those of the heart in the frog and the tortoise.

The present experiments show that the changes observed when the frog's heart remains *in situ* and supplied by blood are precisely similar to those known to occur in the mammalian heart, they also bring out a further new point of no little interest, since, under certain conditions, a return wave of activity proceeding from the apex to the base is clearly demonstrable; this wave succeeds that which proceeds from the base to the apex. It is this return wave which is largely responsible for the extensive terminal phase of the whole electromotive effect in the beating heart.

The observations now carried out have been made under a considerable variety of conditions, only a few of which can be at present referred to. The recording instrument employed was the extremely sensitive electrometer used by myself for the investigation of nerve. In order to indicate its sensitiveness, I may state that with one contact on a locally injured surface the full change under the other uninjured contact caused a very extensive displacement of the mercury meniscus which, when magnified by the lens used for its projection upon the recording photographic plate, displayed itself as a movement of from 150 to 180 mm.

The heart of the pithed frog was carefully exposed and left covered by pericardium; two contacts were then placed, one across the auriculo-ventricular groove, the other upon the ventricle apex. Each natural beat of the heart, thus left *in situ*, was associated with electromotive changes which caused electrometer movements of the character shown in fig. 2. In the right hand of this curve is the commencement of a heart beat, the rise of the curve indicating the relative negativity of the tissue under the contact upon the groove; the point (*a*) is the commencement of the auricular contraction, the point (*b*) the commencement of the ventricular contraction 0''·46 later. In the left part of fig. 2 the whole of the main ventricular change is displayed; it begins at the point (*b*) and commences to subside at the point

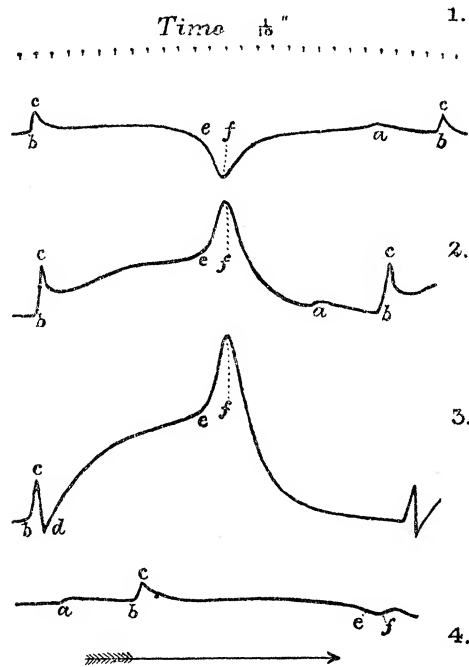
(*f*). The successive events comprise an initial rise at (*b*) (negativity of the base), then a sudden fall at (*c*), occurring 0''·04 later; this gradually ceases, and after some little time a final or terminal rise (negativity of the base) recommences at (*e*). Such a record indicates that the base activity, commencing at (*b*) and beginning to subside at (*f*), is maintained longer than the apex activity which commences at (*c*) and begins to subside at (*e*); the duration of the base activity in this case was 1''·24, that of the apex activity was 1''·08. The curve is in all essentials similar in character to that already referred to as obtained from the mammalian heart *in situ*, both the first, or initial, phase and the second, or terminal, phase having the same sign. Similar records of less extent were obtained when the contacts were appropriately placed upon the external body wall of the frog without exposing the heart, whilst similar ones of larger extent were obtained when the pericardium was opened and the contacts placed upon the actual cardiac surface. If the heart is excised, then the records gradually change in character until ones of the character shown in fig. 1 may be obtained; these correspond in type with those described by Burdon-Sanderson as obtained from the immobile excised heart aroused by an artificial stimulus. It is, however, certain that the diphasic effect with phases of opposite sign, such as that shown in fig. 1, is not characteristic of the frog's heart when examined *in situ*, supplied with blood and beating naturally.

An interesting modification in the type of the records occurs if the ventricle is distended with blood; such distension is readily produced by slight pressure upon the vessels leading from the truncus arteriosus. In order to obtain the modification, the contact upon the groove is now so placed as to comprise that portion of the ventricle base which lies near the exit of the aorta. The modification is shown in fig. 3, which gives one full ventricular change. At the point (*b*) the base negativity due to activity of this part commences, the rise is cut short, as before, at the point (*c*), 0''·05 later, this being due to the propagation of the active state from the base to the apex and the commencement of the apex change; the apex change is, however, itself now cut short at the point (*d*) by a third change occurring about 0''·05 later, and this last change is of the same type as the initial base one, *i.e.*, indicates a second development of base negativity. On the subsidence of the apex effect, which begins at the point (*e*), these two more prolonged base effects, being in the same direction, are summated and produce the conspicuous terminal phase which culminates at the point (*f*). There is no doubt that the period from (*b*) to (*e*) indicates the time taken by the wave of activity in its propagation from the base to the apex, in this instance (temp. 12° C.) at a rate of from 130 to 140 mm. in 1 second; it follows that

the period from (c) to (d) may be interpreted as the time taken by the propagation of the active state back again from the apex to that part of the base from which the aorta springs, in this instance also at a rate of from 130 to 140 mm. in 1 second.

Control experiments, with a contact upon the aortic bulb, showed that this second reversal was not due to the development of electromotive changes in the aortic wall or bulb, these being too feeble to affect the recording instrument. Moreover, although curves showing double reversals of the type shown in fig. 3 are obtained when the heart begins to get distended with blood, if, by further aortic compression, this distension becomes considerable, then the records tend to return to the type indicated in fig. 1, the ventricle base effect near the aorta being now almost imperceptible; on removing the distension and letting the blood out of the swollen heart by cutting through the bulb, curves of the type shown in fig. 3, with the double reversal of the first phase, are again obtained. It thus appears that adequate blood supply through intracardiac pressure brings into prominence the activity of that part of the ventricle which leads up to the aorta, and that this favourable influence, although interfered with by considerable distension, continues after the blood has left the heart; hence the new phenomena of double reversal are not directly caused by intraventricular blood pressure, but are indirectly associated with a previous adequate blood supply of the muscular tissue forming the ventricular wall. A number of experiments carried out with different positions of contacts and under a variety of conditions (local slight injury, local warming, etc.) have convinced me that the cause of the double reversal is the circumstance that, during the ventricular contraction, a wave of activity starts in that part of the base which is not immediately related to the aortic exit, and that this, having been propagated to the apex, then returns from the apex to the aortic part of the base.

Only one class of such experiments need be referred to in this preliminary communication. If contacts are placed on each lateral margin of the base near the groove, so that one lies upon the left side remote from the aorta, the other upon the right side near the spring of the aorta, then each natural beat of the heart is associated with electromotive effects of the type shown in fig. 4; these become more and more pronounced under the special conditions which favour the appearance of the double reversal. The curve given in fig. 4 shows the auricular beat commencing at the point (a); this is followed after an interval of 0''·45 by the base effect which begins at the point (b). Now, since the rise of the curve indicates relative negativity of the tissue under the contact on the left margin of the groove, which is remote from the aortic exit, it is clear that the change activity must commence here



DESCRIPTION OF FIGURES.

The curves given in the above figures are outlines of four photographic records of the displacement of the capillary electrometer meniscus. On each figure a rise in the curve indicates relative negativity of the tissue under a contact upon the auriculo-ventricular groove; all the curves are to be read from left to right.

FIG. 1.—Excised frog's heart, contacts upon auriculo-ventricular groove and upon the ventricle apex; natural beats; (a) auricular activity, (b) commencement of ventricular activity at base of ventricle, (c) commencement of ventricular activity at apex of ventricle, (f) summit of final ventricular phase.

FIG. 2.—Frog's heart *in situ*, contacts as in fig. 1; (a) commencement of auricular activity, (b) commencement of ventricular activity at base, (c) commencement of ventricular activity at apex, (f) summit of final phase.

FIG. 3.—Frog's heart *in situ*, but during or after distension with blood, contacts on ventricle base near spring of aorta and on ventricle apex; (b) commencement of general base activity, (c) commencement of ventricular activity at apex, (d) commencement of base activity localised to neighbourhood of aorta, (f) summit of final ventricular phase.

FIG. 4.—Frog's heart *in situ*, contacts on each side of base near groove, one on left side remote from aorta, the other on right side close to spring of aorta; (a) commencement of auricular activity, (b) commencement of activity under contact on left side of base remote from aorta, (c) commencement of activity on right side of base near aorta.

before a similar change commences under the other contact, that is, in the tissue near the aortic exit. The rise is, however, cut short at the point (c)

by the commencement of such a change under the aortic base contact; this occurs in a number of measured records after a delay of from 0''·06 to 0''·08, *i.e.*, a longer interval than can be accounted for by the propagation time from base to apex. Moreover, the base change which commences first at (*b*), subsides first at (*e*), that commencing later at (*c*) subsiding later at (*f*), and thus causing a second or terminal phase of opposite sign to the first, or initial, one. Many records of this type have been obtained, and in every instance the first phase is of the same character; hence in the natural beat the whole base does not pass simultaneously into the active state with its associated relative negativity, the manifestation of such activity in the part near the exit of the aorta being always delayed.

The development of the frog's heart from a primitive **S**-shaped tube, and the well-known fact that a contraction of the wall of the aortic bulb occurs as the last stage of the whole cardiac cycle, are in accordance with the observations now described. These show that the frog's heart, when fully developed, continues to display signs of its ontogeny, and that even when these are structurally imperceptible, they can be revealed by appropriate physiological methods.

[The experiments here described were all carried out upon winter specimens of *Rana temporaria* during the months of January, February, and March.]
